Significance of macroalgal polymorphism: intraspecific tests of the functional-form model

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Abstract

The functional-form model, developed for comparisons among species in a diverse macroalgal community, was used to examine the functional significance of macroalgal polymorphism (i.e., the existence of genetically distinct morphotypes within a single species). Four predictions of this model were examined along a continuum of morphotypes represented by eight clones of the red alga *Gracilaria tikvahiae* McLachlan. These clones had significant differences in calorific content, percentage of photosynthetic tissue, net photosynthesis, and specific growth rate. All of these functional attributes were a function of the surface area:volume ratios. Consistent with the predictions of the functional-form model, clones near opposite ends of the surface area:volume continuum had significant differences for these attributes. A cluster analysis of these attributes identified three clusters of clones that agreed well with their surface:volume ratios. Polymorphism in *G. tikvahiae* increases the ecological and physiological fitness of this species in an estuarine system where spatial and temporal changes in the environment occur. Each morphotype possesses concomitant, ecologically meaningful combinations of benefits and costs which collectively spread the risk from different sources of mortality and thus increase the overall survival of the population.

Introduction

The functional-form model was developed to synthesize the adaptive significance of thallus form relative to productivity ecology and survival of benthic macroalgae (Littler and Littler 1980). The functional-form model has been used to understand and predict ecological patterns within a diverse macroalgal flora (Littler 1980, Gaines and Lubchenco 1982, Littler and Arnold 1982, Norton et al. 1982, Steneck and Watling 1982, Littler et al. 1983, Rosenberg and Ramus 1984). The basic assumption of this model is that algal ecologists can use form-function relationships as indicators to interpret community stability/disturbance patterns and to

identify the important environmental or biotic factors without detailed demographic studies at the species level (Littler and Littler 1984). The functional-form approach should be applicable anywhere the predominant algal abundances are known without being restricted by phylogenetic group, habitat, or geological era (e.g. see Gaines and Lubchenco 1982, Steneck and Watling 1982).

Although such a *between-species*, comparative approach appears valid for a broad spectrum of macroalgae (e.g. Steneck and Watling 1982, Littler et al. 1983), the functional-form model has not been tested on different morphological forms *within* a species. Such a test could add considerable insight into the ecological and functional significance of intraspecific thallus-form variations.

The species studied was the red alga *Gracilaria tikvahiae* McLachlan, which is an important component of macroalgal communities in coastal lagoons along the eastern coast of North America, from Prince Edward Island to Florida (Taylor 1957, 1960, McLachlan 1979). Throughout its large geographical range, populations of *G. tikvahiae* exhibit a high degree of morphological variability (Kim and Humm 1965, Chapman et al. 1977, McLachlan 1979). This may be due to a relatively high spontaneous mutation rate; mutations are readily induced by artificial means (Van der Meer 1979).

A series of predictions (Table 1) and hypotheses were derived for *Gracilaria tikvahiae* from those developed for interspecific tests of the functional-form theory (Littler and Littler 1980). Neither the morphological attributes nor the predictions listed in Table 1 are mutually exclusive due to the complex interactions found at the organismal level. As surface area:volume ratio is the result of numerous morphological features of algae and likely to have ecological and physiological significance (e.g. Odum et al. 1958, Gutknecht 1961, Rosenberg and Ramus 1984), this ratio was used as a first approximation of an integrated measure of morphology that could be related to algal function. In this communication, the tests of several of these hypotheses are presented.

Table 1. *Gracilaria tikvahiae*. Morphological attributes and predictions. Based on concepts presented by Littler and Littler (1980) and on the hypotheses proposed in the text, the different morphological types present within populations of *G. tikvahiae* should ideally form a continuum. Expected morphological attributes and predictions resulting from these interdependent hypotheses are described for the extreme ends of the continuum. In the current study, hypotheses were developed to test Predictions 1–4

		Simpler, more delicate forms	Larger, coarsely-branched forms
Morphological attributes			
(1)	Surface area:volume ratio	Higher	Lower
(2)	Branching frequency	Higher	Lower
(3)	Size of branches	Smaller	Larger
(4)	Differences in thallus thickness between older and newer parts of thalli	Not significant	Significant
Predictions			
(1)	Calorific content	Higher	Lower
(2)	Structural		
	proportion of photosynthetic to total volume of plant tissue	Higher	Lower
	energy spent on production of structural compounds	Lower	Higher
(3)	Photosynthesis/growth		
	photosynthesis per unit biomass	Higher	Lower
	net production	Higher	Lower
(4)	Growth rates	Higher	Lower
(5)	Nutrient uptake: capacity for nutrient uptake, particularly at lower nutrient concentration	Higher	Lower
(6)	Predation: susceptibility to grazing	Higher	Lower
(7)	Resistance to physical environmental disturbances	Lower	Higher

Materials and methods

Clones

Strains of *Gracilaria* spp. were isolated from the Indian River Lagoon, Florida, and placed into outdoor tank cultivation as previously described (Ryther et al. 1981, Hanisak and Ryther 1984, Hanisak 1987). Clonal isolates were made from outdoor cultures and reared in laboratory cultures. These cultures were used to inoculate small (107 liters) tank cultures in a greenhouse prior to being transferred to outdoor tanks (1.7 m² in surface area, ca. 750 liters in volume). All clones were grown under identical conditions in these tanks, receiving ca. eight exchanges of Indian River seawater per day, continuous aeration, and weekly nutrient enrichments standardly employed for the cultivation of *Gracilaria* (Hanisak 1987).

From the clones available, eight were identified as *Gracilaria tikvahiae* (McLachlan 1979) and used in this study. These clones are representative of the haploid, vegetatively propagating forms found in the Indian River Lagoon, and encompass the range of morphology observed for the cultivated strains, but not necessarily the full range that occurs naturally.

Surface area:volume measurements

Triplicate measurements of thallus volume and surface area were made for portions of ten individual plants for each clone. Thallus volume was determined to 0.01 cm³ by submergence in an Erlenmeyer flask and measurement of the volume of water displaced upward in the narrow neck using a suction microburette. The projected two-dimensional surface area of each thallus was determined to 0.001 cm² with a Li-Cor Model 3100-1+1 area meter. The total surface area of each thallus was determined by multiplying the projected surface area by an appropriate conversion factor. For example, the surface area of cylindrical branches was obtained by multiplying the projected surface area by π. When necessary, portions of the thalli were dissected and the surface areas of the dissected parts summed to obtain the total surface area.

Calorific hypothesis

Statement of hypothesis. Calorific content increases with increasing surface area:volume ratio due to a decrease in structural compounds and an increase in more metabolically-active, high-energy compounds.

Background. Paine and Vadas (1969) found that algal calorific values correlated with ranking for thallus longevity (i.e., emphemeral > annual > perennial). Littler and Murray (1978) also substantiated this finding, but interpreted the relationship more directly in terms of morphological form. Macroalgae, such as *Lithothrix aspergillum*, which contain a

high ratio of structural to photosynthetic tissues (presumably of selective advantage in interference competition for space, light, or protection from predation or physical stress), may have relatively less energy to allocate toward rapid growth and reproduction. Littler and Murray reported low calorific values for epilithic encrusting forms [e.g. *Pseudolithophyllum decipiens* (= *Hydrolithon decipiens*), *Pseudolithoderma nigra, Ralfsia* sp.]. Larkum et al. (1967) and Paine and Vadas (1969) believed that calcification and low calorific content may be important for survival under conditions of high grazing pressure by decreasing the energetic yield to the herbivore. Littler et al. (1983) and Littler and Littler (1984) noted a great reduction in calorific content for crustose and articulated algae even when corrected for the high ash contents. Early-successional delicate forms are higher in calorific content than other fleshy algae.

Methods. Samples ($n \geq 5$) of the clones were cleaned, briefly rinsed in distilled water, and dried to constant weight at 80 °C. The algae were then ground to a fine powder, pelletized, and three replicates ignited in a Parr (Model 1243), automated, semimicro, adiabatic, oxygen bomb calorimeter. The data were expressed as cal g^{-1} ash-free dry wt (kJ g^{-1} ash-free dry wt). Ash-free dry weight was determined as the weight loss in dried algal samples after combustion at 500 °C for 8 h in a muffle furnace.

Structural hypothesis

Statement of hypothesis. The proportion of photosynthetic tissue in the thallus increases with increasing surface area:volume ratio due to a decreased allocation of materials to structural components.

Background. The allocation of materials to structural versus photosynthetic tissues has not been considered except by Kanwisher (1966), Littler (1980), and Littler and Littler (1980).

Methods. Cross-sections about one cell thick were made with an American Optical cryostat microtome from three different regions of the thallus (basal, medial, and apical) for each of ten individuals of every clone. The diameters of the non-photosynthetic and photosynthetic areas transected were determined with a compound microscope. For each region of each plant, the percentage of the total cross-sectional area that was pigmented was calculated. The percent photosynthetic area was estimated for each plant by averaging the three measurements made along each thallus.

Net photosynthesis and growth hypotheses

Statement of hypothesis. Apparent net photosynthetic and specific growth rates increase with increasing surface area:volume ratio due to an increased allocation of resources to photosynthetic apparatus at the expense of structural components.

Background. Littler (1980) found that 45 species of temperate macroalgae, in thallus-form groups from highest to lowest producer on a dry weight basis, ranked as follows: thin sheet-like forms, finely-branched forms, coarsely-branched forms, and prostate epilithic forms. Odum et al. (1958), Kanwisher (1966), King and Schramm (1976), and Littler and Arnold (1982) noted that finely-branched forms had higher production rates than coarsely-branched species. A thallus-form more suited to obtaining light energy and nutrients would seem to explain the differences. Apparent net photosynthesis is directly correlated (e.g. Wassman and Ramus 1973, Brinkhuis 1977) with potential for growth and represents a rapid and effective measure of one component of fitness when determined under field conditions. The thallus-form/productivity relationship is applicable (Littler 1980) over a broad range of habitats. Therefore, selection pressure for small thallus-forms with rapid growth and high reproductive output (*r*-selection *sensu* Pianka 1970) in addition to selection for larger, slower-growing morphological forms with potentially enhanced competitive or stress-tolerant abilities (*C*- and *S*-selection, respectively, *sensu* Grime 1977) [as well as disturbance-tolerant and predation-resistant strategies (*D*-selection and *P*-selection, respectively, *sensu* Littler and Littler 1984)] appear to be widespread evolutionary forces among the macroalgae.

Photosynthetic methods. Side-by-side comparative measurements of net photosynthesis were made for all clones of *Gracilaria tikvahiae* (four to six replicates each). All plants used were macroscopically free of epiphytes. Incubations were carried out between 09.00 and 15.00 hrs under natural *in situ* conditions. Thallus weight:water volume:incubation-time ratios did not exceed the threshold of limiting factors (Littler 1979). Mixing was continuous by means of water-driven magnetic turbines and was above the saturation level for water movement. Net productivity was calculated as mg C fixed g^{-1} dry algal wt h^{-1}, mg C g^{-1} fixed ash-free dry wt h^{-1}, and g C m^{-2} of algal thallus h^{-1}. The methods concerning the handling of algae, incubation, and oxygen analysis followed those recommended by Littler (1979), except that an Orbisphere Laboratories Model 1459 O$_2$ analyzer was used.

Growth methods. Seven clones of *Gracilaria tikvahiae* were cultured under a range of temperatures, salinities, and photon flux densities, and specific growth rates were measured. Small, clean, growing tips were isolated from stock cultures into culture dishes containing Provasoli's enriched sea-water (PES; Provasoli 1968), without vitamins. The day before each experiment, apical tips, 20 mm in length, were cut from the appropriate clones and placed into culture dishes. On the day each experiment began (i.e. Day 0), individual apical tips were blotted with a tissue paper to remove excess water, weighed to the nearest 0.1 mg on an analytical balance, and placed into a culture dish containing 200 ml of
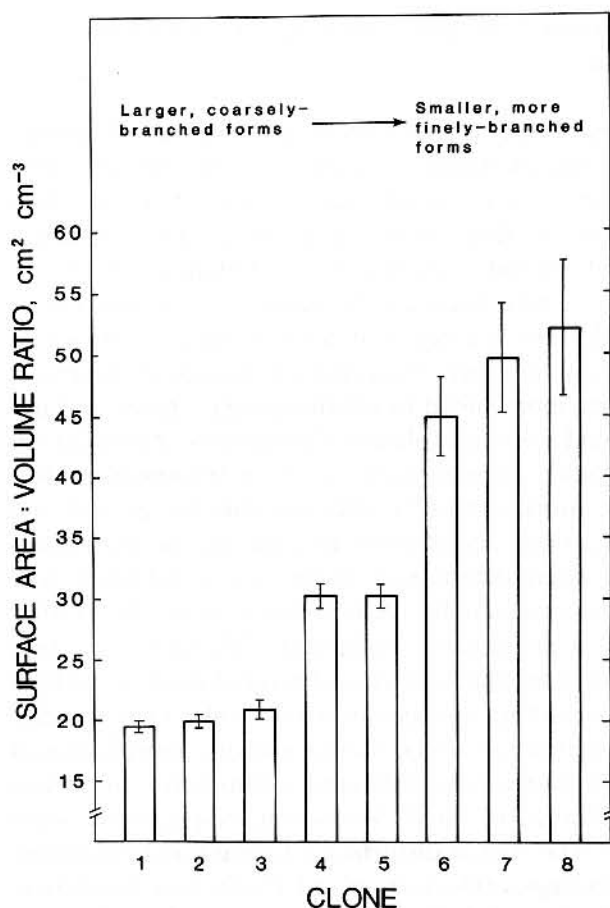
Fig. 1. *Gracilaria tikvahiae.* Surface area:volume ratios of eight clones from outdoor tank cultures. Data are means ± 1 standard error ($n = 10$)

PES under the appropriate experimental conditions. The medium was changed every 7 d, when the blotted wet weight was measured. After 21 d, the experiments were terminated and dry weights were determined (after at least 48 h at 80 °C). Initial dry weights were estimated by measuring the percent dry weight of additional apical tips ($n = 3$) and multiplying this value by the initial blotted wet weight. From the initial (Day 0) and final (Day 21) measurements of dry weight, specific growth rates were calculated from the equation:

$$k = \frac{\log_2 (W_t/W_i)}{t},$$

where k = the specific growth rate, expressed as biomass doublings d^{-1}, W_i = the initial weight of the thallus, and W_t = the weight of the plant after t number of days. Maximal growth rates for all cultures were found under the following range of conditions: 24° to 30 °C, 24 to 36‰ S, 100 to 200 µE cm^{-2} s^{-1} of cool-white fluorescent light, under a photoperiod of 14 h light:10 h dark.

Statistical analyses

Means are presented with standard errors. Statistical significance of differences between means was determined with analysis of variance (ANOVA). Comparisons among means

were made with Tukey's method, referred to as the T-method, at the 0.05 level (Sokal and Rohlf 1981). Because a continuum of surface area:volume ratio was observed for the clones, the data for each hypothesis were plotted as a function of this ratio and a linear regression analysis was performed. A correlation matrix of surface area:volume ratios, calorific contents, percent photosynthetic areas, net photosynthetic rates, and specific growth rates for the eight clones of *Gracilaria tikvahiae* was obtained and statistical significance of the resulting correlation coefficients was assessed (Sokal and Rohlf 1981). Because differences among clones for various morphological and functional attributes might co-vary with differences in surface area:volume ratio, an analysis of covariance (ANCOVA) was performed with BMDP statistical software (Dixon 1983) for all parameters measured.

To test the overall postulate relating functional-form to ecological and physiological parameters, a multiparameter cluster-analysis of clones was performed. The percent photosynthetic areas, calorific contents (on an ash-free dry weight basis), photosynthetic rates (on an ash-free dry weight basis), and growth rates for all possible pairs of clones were compared by the Euclidean distance coefficient following a transformation of the data to proportions, and then subjected to hierarchical cluster analysis by the unweighted pair-group method (Sneath and Sokal 1973, Romesburg 1984). This cluster analysis was performed using the SYSTAT statistical package (Wilkinson 1986) on an IBM microcomputer.

Results

Surface area:volume measurements

Surface area:volume ratios for the eight clones of *Gracilaria tikvahiae* ranged from 19.5 ± 0.5 to 52.3 ± 5.5 cm^2 cm^{-3} (Fig. 1). These differences were highly significant (ANOVA, $P < 0.001$). These clones fell into three distinct groups based on their surface area:volume ratios (T-method, $P < 0.05$). Three clones, designated 1, 2, and 3, had surface area:volume ratios of approximately 20. Two clones, 4 and 5, had surface area:volume ratios of approximately 30. Three clones, 6, 7 and 8, had surface area:volume ratios of 45 to 52. Clones of *G. tikvahiae* with higher surface area:volume ratios were highly branched with many smaller, finer branches; clones with lower surface area:volume ratios were thicker, more coarsely branched forms that were almost cartilaginous in texture.

Calorific measurements

The calorific content for the eight clones of *Gracilaria tikvahiae* (Table 2, Fig. 2A) ranged from $2\,204 \pm 10$ to $2\,695 \pm 9$ cal g^{-1} dry wt (9.22 ± 0.04 to 11.3 ± 0.04 kJ g^{-1} dry wt),

A

CALORIFIC CONTENT, cal g^{-1} dry weight

2700 •6
2640 •8
2580 •5 •7
2520
2460 •4
2400
2340 •1
2280
2220 •3 •2

$y = 12.2x + 2058$
$r^2 = 0.77$
$p = 0.002$

B

CALORIFIC CONTENT, cal g^{-1} ash-free dry weight

•6 4800
•5 •8 4500
•4
•7 4200
3900
•1 3600
•3 •2

$y = 30.6x + 3172$
$r^2 = 0.55$
$p = 0.034$

C

ORGANIC CONTENT, % of dry weight

0.64 •2
•1 •3
0.62
0.60 •7
0.58 •8
0.56 •4,5 •6

$y = -0.0015x + 0.6432$
$r^2 = 0.28$
$p = 0.183$

D

% PHOTOSYNTHETIC AREA

•7 0.30
•6 •8
•5 0.27
0.24
•3 0.21
•4
•2 0.18

$y = 0.0036x + 0.1224$
$r^2 = 0.78$
$p = 0.005$

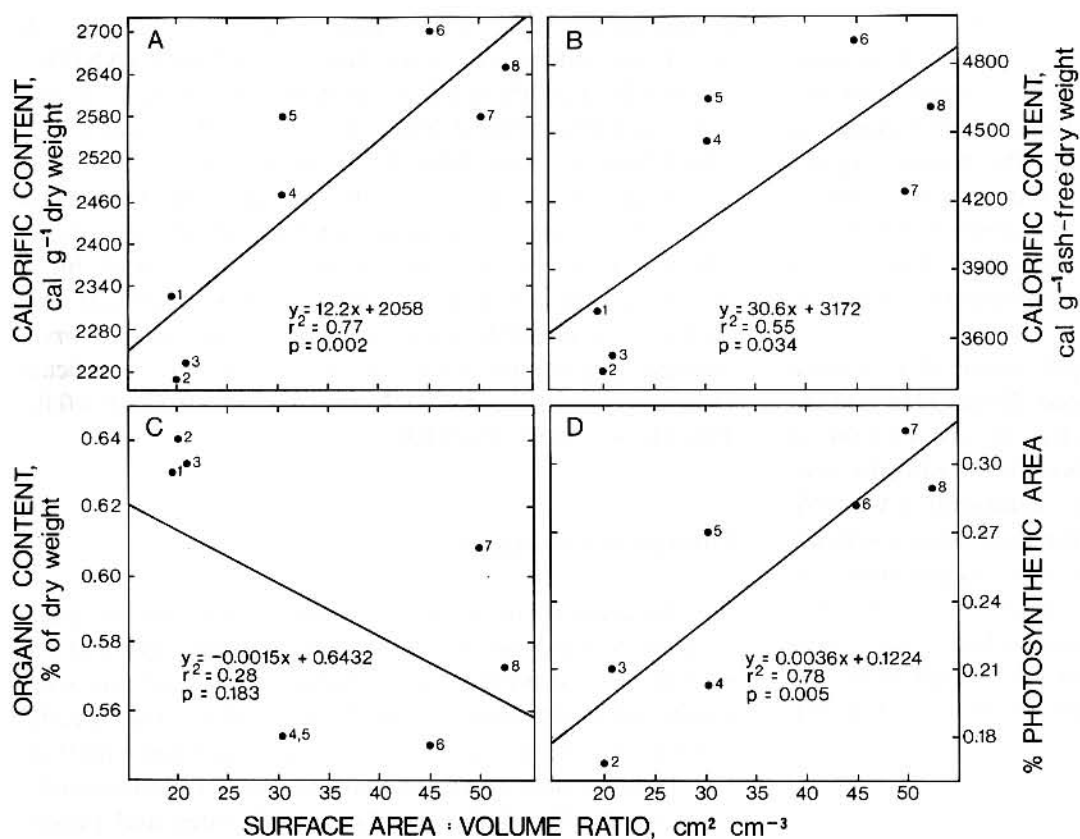SURFACE AREA : VOLUME RATIO, cm^2 cm^{-3}
(20 25 30 35 40 45 50)

Fig. 2. *Gracilaria tikvahiae*. Regression analysis of calorific content on dry weight (A) and ash-free dry weight (B) bases, organic content (C), and percent photosynthetic area (D) against surface area:volume ratios for eight clones. Numbered data points indicate mean values for the attributes of the clones bearing same numbers in Fig. 1

Table 2. *Gracilaria tikvahiae*. Comparative morphological and functional attributes of eight clones. Data are means ± 1 standard error (n). nd: no data

Attribute	Clone No.:							
	1	2	3	4	5	6	7	8
Calorific content								
cal g^{-1} dry wt	2 324	2 204	2 236	2 478	2 575	2 695	2 576	2 649
	±17	±10	±11	±15	±8	±9	±25	±8
	(7)	(5)	(5)	(5)	(6)	(6)	(8)	(6)
cal g^{-1} ash-free dry wt	3 696	3 449	3 539	4 474	4 664	4 910	4 236	4 631
	±26	±15	±17	±27	±15	±16	±40	±14
	(7)	(5)	(5)	(5)	(6)	(6)	(8)	(6)
Organic content								
% of dry wt	62.88	63.90	63.17	55.30	55.21	54.88	60.82	57.21
	±3.96	±0.16	±2.81	±2.09	±0.21	±0.80	±0.28	±0.24
	(6)	(5)	(6)	(5)	(5)	(4)	(5)	(6)
Percent photosynthetic area	nd	17.06	21.15	20.16	27.06	28.19	31.57	28.91
	nd	±0.97	±1.40	±1.06	±0.82	±1.78	±1.62	±2.07
	nd	(10)	(10)	(10)	(10)	(10)	(10)	(10)
Net photosynthetic rate								
mg C g^{-1} dry wt h^{-1}	1.52	4.40	3.77	6.76	7.23	7.81	8.04	12.23
	±0.21	±0.31	±0.19	±0.28	±0.29	±0.10	±0.30	±0.35
	(6)	(5)	(6)	(5)	(5)	(4)	(5)	(6)
mg C g^{-1} ash-free dry wt h^{-1}	2.46	6.88	6.05	12.33	13.10	14.24	13.23	21.37
	±0.36	±0.49	±0.47	±0.78	±0.55	±0.30	±0.54	±0.60
	(6)	(5)	(6)	(5)	(5)	(4)	(5)	(6)
g C m^{-2} of thallus h^{-1}	0.08	0.29	0.35	0.60	0.68	0.59	0.59	0.65
	±0.01	±0.02	±0.02	±0.02	±0.04	±0.04	±0.02	±0.03
	(6)	(5)	(6)	(5)	(5)	(4)	(5)	(6)
Specific growth rate								
doublings d^{-1}	nd	0.112	0.139	0.154	0.177	0.133	0.234	0.231
	nd	±0.003	±0.003	±0.007	±0.004	±0.002	±0.003	±0.003
	nd	(9)	(9)	(9)	(9)	(9)	(9)	(9)

with the highest calorific contents found in those clones with the highest surface area:volume ratios. The organic content per unit dry weight for the different clones ranged from 54.9 to 63.9% (Table 2, Fig. 2C). The three clones having the lowest surface area:volume ratio had the highest organic content. The regression of organic content versus surface area:volume ratio for all clones was not significant (Fig. 2C; $r^2 = 0.28$, $P = 0.183$). The organic content of these clones was significantly different (arcsine transformation ANOVA, $P < 0.01$).

The calorific content for the eight strains of *Gracilaria tikvahiae* (Table 2, Fig. 2B) ranged from 3449 ± 15 to 4910 ± 16 calories g^{-1} ash-free dry wt (14.4 ± 0.06 to 20.5 ± 0.07 kJ g^{-1} dry wt). Differences in the calorific content of these clones were highly significant (ANOVA, $P < 0.001$). The calorific content of the three strains with the lowest surface area:volume ratios were significantly (T-method, $P < 0.05$) lower than the other five strains. The regression of calorific content versus surface area:volume ratio for all clones was significant, on a dry weight (Fig. 2A; $r^2 = 0.77$, $P = 0.002$) and an ash-free dry weight (Fig. 2B; $r^2 = 0.55$, $P = 0.034$) basis.

Structural measurements

For any clone, differences in the proportion of cross-sectional area allocated to pigmented tissue among the basal, medial, and apical sections of the plant were not statistically significant (ANOVA, $P > 0.05$). Consequently, the data for these three sections were averaged and the ratio of the pigmented (i.e., photosynthetically active) area to the total cross-sectional area of the thalli was calculated for seven clones of *Gracilaria tikvahiae* (Table 2, Fig. 2D). Differences in the percentage of photosynthetic tissue in these clones were highly significant (ANOVA, $P < 0.001$). These differences were due more to changes in the amount of structural, non-photosynthetic tissue than to changes in the absolute photosynthetic area of the clones. The percent photosynthetic area of the three clones with the lower surface area:volume ratios was significantly lower (T-method, $P < 0.05$) than the four with the higher surface area:volume ratios. The former group had an average photosynthetic area of 19% of the total cross-sectional area (with a range of 17 to 21%), whereas the average of the latter group was 29% (with a range of 27 to 32%). The regression of percent photosynthetic area versus surface area:volume ratio for the clones measured was significant (Fig. 2D; $r^2 = 0.78$, $P = 0.005$).

Net photosynthesis measurements

Similar trends were observed for net photosynthetic rates relative to dry weight and ash-free dry weight. Net photosynthetic rates varied by an order of magnitude (i.e., 1.5 to 12.2 mg C g^{-1} dry wt h^{-1} or 2.5 to 21.4 mg C g^{-1} ash-free dry wt h^{-1}) for the eight clones and increased as a function of increasing surface area:volume ratios (Table 2; Fig. 3A, B). These differences were highly significant (ANOVA, $P < 0.001$). For these photosynthetic rates based on biomass, four groupings (Clone 1; Clones 2 and 3; Clones 4–7; and Clone 8) were defined (T-method, $P < 0.05$). These groupings are consistent with an increase in surface area:volume ratios. The same trend was observed with net photosynthetic rates calculated on an areal basis (Table 2, Fig. 3C), although differences between clones were reduced. Regressions of all three measures of photosynthesis versus surface area:volume ratio for all clones were significant (Fig. 3A, $r^2 = 0.79$, $P = 0.02$; Fig. 3B, $r^2 = 0.77$, $P = 0.02$; Fig. 3C, $r^2 = 0.53$, $P = 0.036$).

Growth measurements

Specific growth rates of seven clones of *Gracilaria tikvahiae* in laboratory cultures varied by more than two-fold (0.11 to 0.23 biomass doublings d^{-1}) (Table 2, Fig. 3D) and were significantly different (ANOVA; $P < 0.001$). The specific growth rates of these clones were highly correlated with their net photosynthetic rates; for example, the correlation coefficient ($r = 0.720$) of the specific growth rates and photosynthesis based on ash-free dry weights was significant ($P < 0.05$). The two clones with the highest surface area:volume ratios had a significantly higher specific growth rate than the other clones (T-method, $P < 0.05$). The regression of specific growth rate versus surface area:volume ratio for the clones measured was significant (Fig. 3D, $r^2 = 0.59$, $P = 0.041$).

Correlation, cluster, and ANCOVA analyses

Calorific contents, percent photosynthetic areas, net photosynthetic rates, and specific growth rates (Table 3) were significantly ($P < 0.05$) or highly significantly ($P < 0.01$) correlated with surface:area volume ratios. These four variables were significantly correlated with each other, except for calorific contents, which were not significantly ($P > 0.05$) correlated with either percent photosynthetic areas or specific growth rates.

Based on the cluster analysis of the calorific contents, percent photosynthetic areas, photosynthetic rates, and growth rates, three clusters of clones were identified (Fig. 4) that agreed well with their surface area:volume ratios (Fig. 1). One cluster (Clones 1, 2 and 3) consisted of the three clones with the lowest surface area:volume ratios; a second cluster (Clones 7 and 8) consisted of the two clones with the highest surface area:volume ratio; the third cluster (Clones 4, 5 and 6) had intermediate surface area:volume ratios. The only significant departure of the cluster analysis (Fig. 4) from the groupings identified solely on the basis of surface area:volume ratio (Fig. 1) was Clone 6. Although this clone had a surface area comparable to Clones 7 and 8, in the cluster analysis it was more associated with the two clones (i.e., 4 and 5) that had intermediate surface
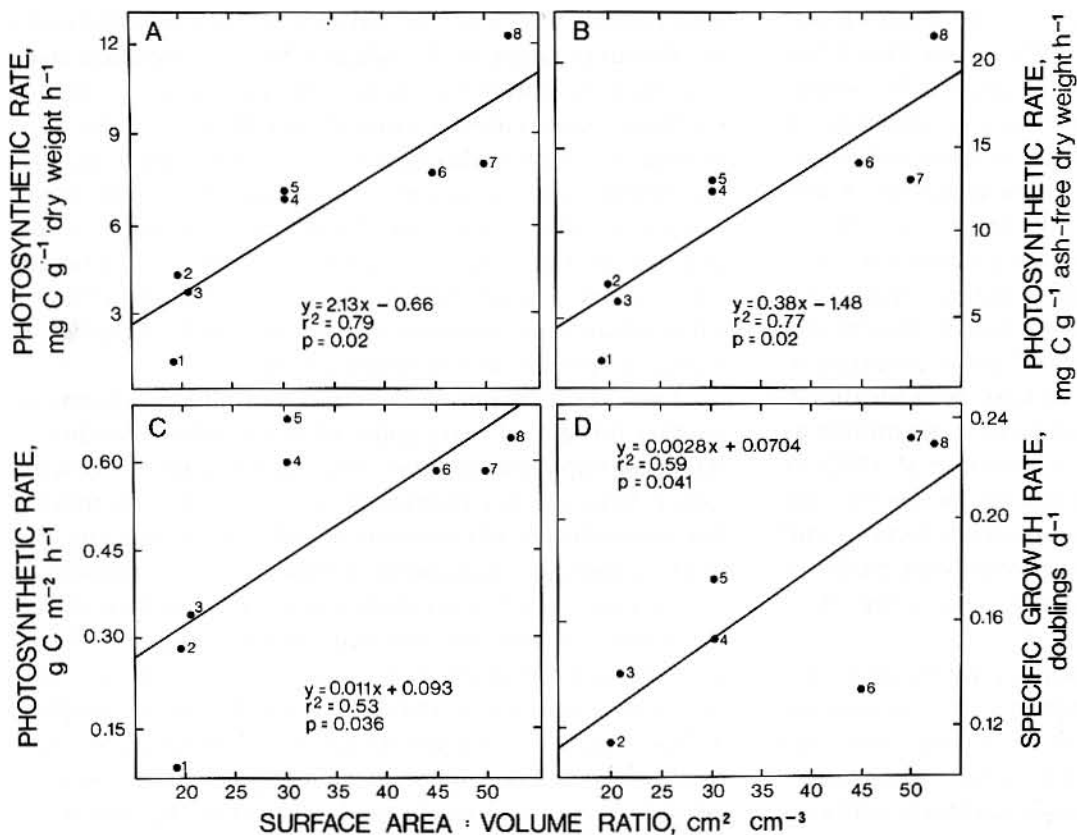
Fig. 3. *Gracilaria tikvahiae*. Regression analysis of net photosynthetic rates on dry-weight (A), ash-free dry weight (B), and areal (C) bases, and specific growth rate (D) against surface area:volume ratios for eight clones. Numbered data points indicate mean values for the attributes of the clones bearing same numbers in Fig. 1
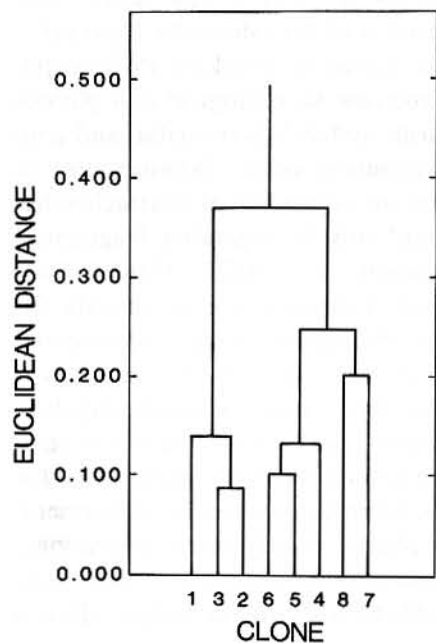

Fig. 4. *Gracilaria tikvahiae*. Cluster analysis of eight clones, based on their calorific contents, percent photosynthetic areas, photosynthetic rates, and growth rates

Table 3. *Gracilaria tikvahiae*. Correlation matrix of surface area: volume ratios (SA:V), calorific contents as cal g^{-1} ash-free dry wt (Cal), percent photosynthetic areas (PPA), net photosynthetic rates as mg C g^{-1} ash-free dry wt h^{-1} (NPS), and specific growth rates as doublings d^{-1} (SGR) for the eight clones used in this study

	SA:V	Cal	PPA	NPS
Cal	0.739*			
PPA	0.884**	0.673[NS]		
NPS	0.878**	0.810*	0.709*	
SGR	0.771*	0.402[NS]	0.782*	0.720*

* Significant ($P < 0.05$)
** Highly significant ($P < 0.01$)
[NS] Not significant ($P > 0.05$)

tically equal ($P > 0.05$) with one exception – photosynthesis measured on an areal basis ($P = 0.019$). This analysis demonstrated the strong dependence of all measured attributes on surface area:volume ratio. The one exception observed would be expected, as surface area was used in the calculation of areal photosynthetic rates.

Discussion

Macroalgal morphology has been examined in respect to ecological and physiological interactions (e.g. Littler 1980, Gaines and Lubchenco 1982, Littler and Arnold 1982, Norton et al. 1982, Steneck and Watling 1982, Littler et al. 1983, Rosenberg and Ramus 1984). The morphological and functional adaptations of an organism to its environment play a critical role in the fitness (survival, growth, and successful

area:volume ratios. This was due primarily to the specific growth rate of Clone 6, which was reduced relative to those of Clones 7 and 8 and comparable to those of Clones 4 and 5.

For the analyses of covariance, data for each attribute were examined versus surface area:volume ratio for the three groupings of clones identified by the cluster analysis. This analysis demonstrated that, when surface:area volume is considered to be the covariant, the adjusted means are statis-

reproduction) of individuals. For example, the matted forms of certain intertidal algae (Hay 1981, Taylor and Hay 1984) confer resistance to predation and desiccation while lowering productivity (Dawes et al. 1978). Crustose alternates in the life histories of frondose algae such as species of *Gigartina* and *Scytosiphon* are thought (Lubchenco and Cubit 1980, Slocum 1980, Dethier 1981, Littler and Littler 1983) to allow persistence under conditions of high herbivory and, possibly, severe wave shock or sand scouring. Specialized internal cytological structures related to tensile strength and extensibility (Koehl and Wainwright 1977) or to adjusting to differing light regimes (Ramus 1978) have been identified. Neushul (1972) related kelp morphology to water motion as an important selective factor (see also Norton et al. 1982). A costs versus benefits approach integrating the diverse features of algal morphology with ecological interactions and physiological functions (i.e., the functional-form model of Littler and Littler 1980) can be used to assess important adaptive strategies.

The major premise of the functional-form model is that all plants have basic energy requirements. Resources committed for morphological differentiation, reproduction, and longevity are not available for other uses, e.g. rapid growth. As morphological complexity increases, certain benefits accrue such as defenses against predation, competition, or environmental stresses. These benefits are balanced by concomitant costs, e.g. reduced photosynthetic potential, growth rate, or reproduction. This model is applicable along broad taxonomic groupings. The intent of the present study was to test the model along a continuum of morphological forms (i.e., "morphotypes") within a single species.

The ecological and physiological significance of surface area:volume ratios has been considered more frequently in the study of phytoplankton (e.g. the review by Sournia 1982) than macroalgae. Although the increased complexity of macroalgae may require more detailed morphometric analysis than phytoplankton, surface area:volume ratios provide an integrative measure of morphological complexity that has functional significance. These ratios relate the potential for the exchange of energy and nutrients (as determined by surface area) to the biomass (i.e., volume) of an organism. It would be expected that processes such as photosynthesis and nutrient uptake would increase with increases in surface area:volume ratios. Significant exceptions to this pattern may include dense aggregations (i.e., turfs) of some filamentous algae (Dawes et al. 1978). The continuum of surface area:volume ratios for the eight clones of *Gracilaria tikvahiae* examined in this study showed that this ratio decreased as morphological complexity increased. The surface area:volume ratio was a good predictor of ecologically and physiologically important attributes in this species.

All of the observations on these clones supported the predictions of the functional-form theory concerning four hypotheses (structural, calorific, photosynthetic, and growth). Because the clones of *Gracilaria tikvahiae* selected represented portions of a continuum, each clone was not statistically different from all others for any one parameter. However, clones near opposite ends of the surface

area:volume ratio spectrum did show significant differences for all four parameters. As indicated by the correlation analysis, the four parameters tested (the percentage of photosynthetic tissue, calorific content, net photosynthesis, and growth rate) were highly interrelated. When cluster analysis was employed to group the clones objectively, this grouping was nearly identical to that based solely on their surface area:volume ratios. Thus, it is concluded that the functional-form model, as proposed by Littler and Littler (1980), is valid within a polymorphic species such as *G. tikvahiae* as well as across broad taxonomic groups.

These clones maintained distinct morphologies from one another for several years under identical culture conditions (Hanisak unpublished data), thus demonstrating a genetic, rather than an environmental, basis for polymorphism. Each morphotype of *Gracilaria tikvahiae* possesses concomitant ecologically meaningful combinations of benefits as well as costs, which collectively spreads the risk from different sources of mortality and thus increases the overall survival of the population. For example, clones with low surface area:volume ratios and greater morphological complexity had a higher allocation of energy and materials to structural components (which presumably enhances survival against grazing and mechanical stresses) at the cost of reduced photosynthetic and growth rates. The converse was true for clones with high surface area:volume ratios. This may explain the significance and persistence of algal polymorphism and phenotypic plasticity in nature. Polymorphism in *G. tikvahiae* may increase its ecological and physiological fitness in an estuarine system where spatial and temporal changes in the environment occur. Because most of these estuarine populations are composed of unattached haploid plants that propagate only by vegetative fragmentation and growth (Chapman et al. 1977, Hanisak unpublished data), such polymorphism would increase the fitness of this species in the absence of sexual reproduction. Thus, components of growth and survival (i.e., increases in biomass, apparent photosynthesis, nutrient uptake capabilities, and predation resistance) take on added significance to the fitness of this species. This minimizes the requirement for data on spore production, fertilization success, recruitment, germination, life-history phases, ploidy levels, phenology, and other long-term demographic parameters that have proven relatively intractable to study in macroalgae (Dixon 1973).

This study establishes the utility of functional-form interpretations of morphological/physiological/ecological relationships at the species level. The functional-form model is leading to a more realistic and utilitarian interpretation of algal form, both within and among macroalgal species. A more intensive study of *Gracilaria tikvahiae* and other polymorphic species by the functional-form approach will lead to a better understanding of the significance of polymorphism in macroalgae.

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